

When Eradication is not an Option: Modeling Strategies for Electrofishing Suppression of Nonnative Brook Trout to Foster Persistence of Sympatric Native Cutthroat Trout in Small Streams

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Abstract.—Subspecies of inland cutthroat trout *Oncorhynchus clarkii* occupy a fraction of their historic ranges, and displacement by nonnative brook trout *Salvelinus fontinalis* is among the greatest threats to existing populations in small, headwater streams. Electrofishing is often used to suppress brook trout and enhance cutthroat trout populations, but these efforts are labor intensive and costly. To help managers more effectively plan and implement brook trout control programs, we used survival estimates from a field experiment to construct matrix population models for both species and linked the models by making the vital rates of young cutthroat trout a function of brook trout density to represent the effect of invasion. We then explored the response of cutthroat trout populations (growth rate [λ] and probability of persistence for 50 years) to brook trout suppression across various levels of electrofishing frequency, sampling intensity, capture efficiency, and brook trout immigration rate. Cutthroat trout ($\lambda = 1.10$) and brook trout ($\lambda = 1.20$) both had moderate to high values of λ when biotic interactions were weak or absent, but the cutthroat trout λ declined markedly ($\lambda = 0.61$) when biotic interactions with brook trout were strong. Model results supported the hypothesis that rapid displacement of cutthroat trout is facilitated by the brook trout's inherent demographic advantage and biotic effects on young cutthroat trout. Where annual brook trout suppression was not possible, the temporal distribution of suppression events within a systematic control design strongly influenced the response of cutthroat trout. The absolute response and cost effectiveness of suppression efforts were influenced particularly by the brook trout immigration rate and also by removal efficiency. Multiple consecutive years of suppression (≥ 3 years) benefited cutthroat trout, but to be effective such suppression should not be interrupted for more than two consecutive years once initiated. Eradication would be ideal, but the maintenance control of brook trout and the management of cutthroat trout in sympatry with brook trout will probably remain among the viable management options for the foreseeable future.

How to address threats from nonnative trout species will remain one of the central issues for conservation and management of indigenous fishes in the western USA and elsewhere (Rahel 2002; Dunham et al. 2004; Fausch et al. 2006). Introgressive hybridization, competition, and predation by nonnative trout have

been implicated in the endangerment of numerous salmonid species, including subspecies of inland cutthroat trout *Oncorhynchus clarkii* (Gresswell 1988; Young 1995; Harig et al. 2000), and may continue to confound attempts to reverse the effects of habitat degradation. For example, brook trout *Salvelinus fontinalis* were introduced into western North America beginning in the late 19th century (MacCrimmon and Campbell 1969) and have since become ubiquitous and abundant (Rahel 2000; Schade and Bonar 2005; Lomnický et al. 2007); their invasions frequently displace native cutthroat trout (Dunham et al. 2002;

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Peterson and Fausch 2003a; but see Adams et al. 2002).

Biologists considering active intervention to reduce threats from invasive species commonly focus on three general approaches: (1) prevention, (2) early detection and eradication, and (3) low-level maintenance or control (Mack et al. 2000; Simberloff et al. 2005). Unfortunately, a given approach may present major challenges or may not be possible in some habitats. For example, brook trout are already widely distributed in western U.S. streams, so prevention is usually not an option. However, further invasions into headwaters can be prevented using isolation management (e.g., Novinger and Rahel 2003), where migration barriers are installed to limit the upstream movement of brook trout into stream reaches or networks occupied by cutthroat trout. Use of barriers to intentionally isolate fish populations generally requires detailed knowledge about habitat requirements and movement patterns (e.g., Harig and Fausch 2002; Morita and Yamamoto 2002; Novinger and Rahel 2003); otherwise, such barriers can do more harm than good (Fausch et al. 2006; Peterson et al. 2008). Worse still are cases where this approach fails because the invader passes a compromised structure or is intentionally introduced above a barrier (Thompson and Rahel 1998; Harig et al. 2000).

Successful eradication of established brook trout populations generally entails direct physical removal using electrofishing or fish toxicants (piscicides), such as rotenone or antimycin. Both techniques can be difficult to implement and must be used in conjunction with isolation management to avoid reinvasion (Fausch et al. 2006). Eradication of nonnative salmonids by electrofishing is expensive because of high labor requirements (e.g., Larson et al. 1986; Kulp and Moore 2000; Shepard and Nelson 2004). This approach may injure native fishes because of repeated electrofishing (Kocovsky et al. 1997) and may be impossible in larger habitats because of low capture efficiency. Fish toxicants are the most effective tool used by fishery biologists to eradicate nonnative trout or undesirable fish species (e.g., Finlayson et al. 2002; Moore et al. 2005), especially in large or complex habitats. Despite the importance of fish toxicant use to native fish conservation, public misconception and social resistance to toxicants can be significant (Finlayson et al. 2005). Moreover, occasional problems with product formulation, manufacture, or supply may periodically limit piscicide effectiveness or availability. Therefore, eradication may not be technically, financially, or politically feasible in every instance where a cutthroat trout population of conservation value is at risk of displacement by brook trout. Maintenance control or

suppression of brook trout may be the best option when the risk of inaction is unacceptable.

Although suppression of brook trout by angling has been attempted, it can prove ineffective at controlling populations (Stelfox et al. 2001) and may possibly reduce native fishes by causing incidental mortalities (Paul et al. 2003). In contrast, electrofishing suppression remains a feasible option because it has been shown to significantly reduce the density of nonnative trout and lead to an increase in native salmonids (e.g., Moore et al. 1983), including inland cutthroat trout (Thompson and Rahel 1996; Shepard et al. 2002; Peterson et al. 2004). However, because of the substantial cost of electrofishing, biologists that are considering this method of brook trout suppression must determine how to apportion limited resources so as to realize maximum benefits.

Toward this end, we built stage-based, stochastic matrix models describing sympatric populations of stream-resident brook trout and cutthroat trout and used the models to (1) show the demographic differences between the species and (2) compare the efficacy of various electrofishing treatments for suppressing brook trout. Demographic information for these population models came primarily from a manipulative field experiment on these two species in small, headwater streams in Colorado (Peterson et al. 2004). The models were used to assess the population response of cutthroat trout to brook trout suppression as a function of (1) frequency and temporal distribution of annual suppression visits over a 50-year period, (2) electrofishing intensity (number of passes) during individual suppression events, (3) electrofishing capture efficiency, and (4) immigration by brook trout. We discuss the general behavior and potential limitations of these models, and we interpret simulation results to provide guidance for fishery biologists interested in electrofishing suppression of brook trout or other nonnative salmonids.

Methods

Matrix Model Formulation

Using a combination of our own data and information from the literature, we constructed stage-based matrix population models for sympatric brook trout and cutthroat trout populations that were representative of populations found in small, central Rocky Mountain streams with mean summer temperatures of 8–12°C (Table 1; Figure 1).

Deterministic cutthroat trout matrix model.—A six-stage model for cutthroat trout (Figure 1A) was primarily based on demographic information from a field experiment with Colorado River cutthroat trout *O. clarkii pleuriticus* in small streams within north-central

TABLE 1.—Descriptions of matrix elements and parameters used in demographic models of native cutthroat trout and nonnative brook trout, and mean values and associated coefficients of variation (CVs) used in stochastic projections. Presence or absence of sympatric brook trout is indicated (where applicable) for cutthroat trout means. Reproductive output for both species assumes equal sex ratios and annual spawning after maturity; FL = fork length.

Model element or parameter	Matrix notation	Mean value (brook trout status)	CV (%)
Cutthroat trout			
Age-0 survival	S_{21}	0.025 (present) 0.318 (absent)	20
Age-1 (juvenile) survival	S_{32}	0.227 (present) 0.421 (absent)	20
Age-2 (subadult) survival	S_{43}	0.356	10
Small-adult (140–170 mm FL) survival	S_{54}	0.356	10
Medium-adult (171–224 mm FL) survival–transition probability ^a	$S_{55} = S_{65}$	0.178	10
Large-adult (225–260 mm FL) survival	S_{66}	0.356	10
Small-adult maturity rate (proportion of females mature in stage)	-	0.75	-
Medium- and large-adult maturity rate	-	1.0	-
Small-adult female fecundity (eggs/female)	-	187	-
Medium-adult female fecundity	-	374	-
Large-adult female fecundity	-	572	-
Egg to age-0 survival from spring spawning to fall census (S_{egg})	-	0.4	20
Adult survival from census to spawning (S_{spawn})	-	0.459	-
Small-adult reproductive output (number of offspring) ^b	F_4	12.9	c
Medium-adult reproductive output ^b	F_5	34.3	c
Large-adult reproductive output ^b	F_6	52.5	c
Brook trout			
Age-0 survival	S_{21}	0.323	20
Age-1 (subadult) survival	S_{32}	0.383	20
Small-adult (130–170 mm FL) survival	S_{43}	0.371	10
Large-adult (171–224 mm FL) survival	S_{44}	0.371	10
Age-1 female maturity rate	-	0.25	-
Small-adult maturity rate	-	0.75	-
Large-adult maturity rate	-	1.0	-
Age-1 female fecundity	-	25	-
Small-adult female fecundity	-	234.5	-
Large-adult female fecundity	-	616	-
Egg to age-0 survival from spawning to subsequent fall census (S_{egg})	-	0.061 ^d	-
Age-1 reproductive output ^c	F_2	0.2	c
Small-adult reproductive output ^c	F_3	5.4	c
Large-adult reproductive output ^c	F_4	18.8	c

^a Survival rate for medium-sized adult cutthroat trout is the same as that for other adults (0.356), but only half of medium adults grow enough to transition to the next stage (i.e., $0.356/2 = 0.178$).

^b Reproductive output (F) for a given stage (i) of cutthroat trout is the product of the sex ratio, maturity, fecundity, S_{spawn} , and S_{egg} . For example, average F for small adults is $F_4 = (0.5)(0.75)(187)(0.459)(0.4) = 12.9$. The F includes terms for S_{spawn} and S_{egg} because the birth pulse occurs in spring, whereas the population census occurs in the fall.

^c In our formulation, stochastic variation in F results from the variation in S_{egg} .

^d S_{egg} is smaller for brook trout than for cutthroat trout because the estimate for brook trout represents survival over an entire year.

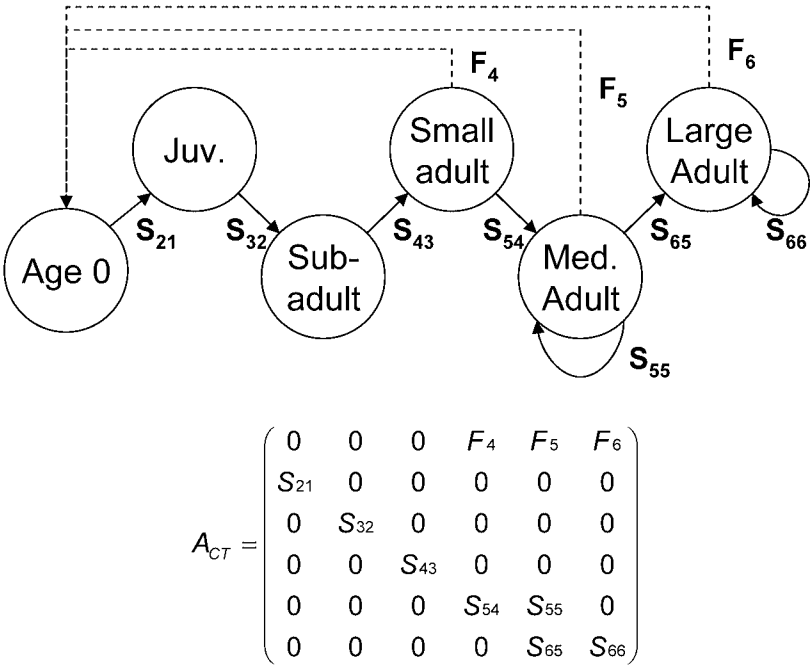
^e F for a given stage (i) of brook trout is the product of the sex ratio, maturity, fecundity, and S_{egg} . For example, average F for small adults is $F_3 = (0.5)(0.75)(234.5)(0.061) = 5.4$.

Colorado (Peterson et al. 2004). Mark–recapture electrofishing was used to estimate the stage-specific survival rates of Colorado River cutthroat trout in two streams where brook trout densities were reduced (treatment streams) and two streams where brook trout densities were not reduced (control streams). Peterson et al. (2004) found that survival of young-of-the-year (age-0) and juvenile (age-1) Colorado River cutthroat trout was markedly higher in treatment streams than in control streams but that adult survival did not differ between treatment and control streams. They inferred that brook

trout invasion caused lower survival of young Colorado River cutthroat trout and that this was a key mechanism leading to displacement of the native species.

The first three stages of the cutthroat trout model—age 0, juvenile, and subadult (age 2)—could be delineated using length frequency histograms from at least two of these streams (e.g., Peterson and Fausch 2002). Three adult stages (small, medium, and large) represent reproductive individuals of various sizes, encompass the range of lengths observed for adult Colorado River cutthroat trout (Peterson and Fausch

A. CUTTHROAT TROUT



B. BROOK TROUT

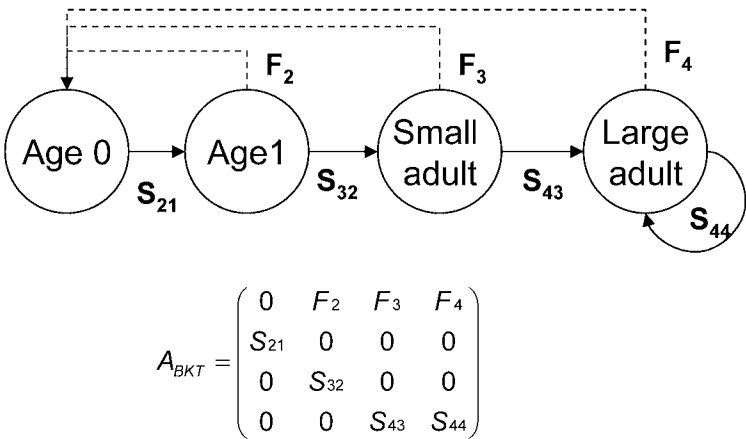


FIGURE 1.—Diagrams of the life cycle and associated matrix representation in stage-based population models for stream-resident (A) native cutthroat trout (CT) and (B) nonnative brook trout (BKT; juv = juvenile stage; med = medium). Table 1 defines the parameter notations and values.

2002), and are consistent with resident populations of other cutthroat trout subspecies (e.g., Downs et al. 1997). Transitions between stages 1–4 (age 0 through small adult) are inevitable, whereas subsequent transitions through size-based stages are inferred from

estimated interannual growth rates of 20–30 mm (D.P.P., unpublished data). Only half of medium-sized adult cutthroat trout (170–224 mm fork length [FL]) transition to the large-adult stage at each time step (Table 1; Figure 1A).

Cutthroat trout survival rates are based on estimates from two mid-elevation streams (Table 5 in Peterson et al. 2004). Mean survival from subadult through all adult stages (0.356) was calculated as the average of survival estimates for ages 2 and older and was shown by the experiment to be unaffected by the presence or density of brook trout (Peterson et al. 2004). In contrast, studies by Shepard et al. (2002; in examining the population response of westslope cutthroat trout *O. clarkii lewisi* to brook trout suppression) and Peterson et al. (2004; in examining Colorado River cutthroat trout population response and direct survival estimates) demonstrated that brook trout reduced the survival of young cutthroat trout when the species were sympatric. Accordingly, we allowed age-0 and juvenile survival rates (S_{21} and S_{32} , respectively) to vary with brook trout density, which was manipulated by electrofishing suppression in the model. High and low values for S_{21} and S_{32} were based on estimates from mid-elevation streams where brook trout were either suppressed or not suppressed (Peterson et al. 2004).

Reproductive output (F), defined as the number of age-0 fish surviving from spring spawning to fall census, was calculated from stage-specific fecundity and maturity, spawning frequency, sex ratio, and survival rates for reproductive adults, eggs, and fry (Table 1). We assumed that (1) female cutthroat trout begin to mature at age 3 or when they reach 140 mm; (2) 75% of the small-adult females and 100% of the medium and large females are mature; (3) mature females spawn each year; and (4) the sex ratio is equal. These maturity thresholds are based on reports for stream-resident populations of other inland cutthroat trout subspecies (Downs et al. 1997; Meyer et al. 2003). Fecundity values were based on an empirical relationship for headwater populations of westslope cutthroat trout (number of eggs per female = $[4.4 \times \text{FL}] - 494.9$, where FL is in mm; Downs et al. 1997) and were calculated for the median sizes of the adult stages.

The model assumes a fall census (e.g., September), whereas cutthroat trout reproduction occurs in early summer (e.g., June). Consequently, cutthroat trout F accounts for adult survival from the previous year's census to spawning (S_{spawn}) over 275 d and for egg to age-0 survival in fall (S_{egg}) over 90 d (Noon and Sauer 1992). These estimates were obtained by rearranging and solving the instantaneous mortality rate equation ($Z = -\log_e[\text{survival}]$) over the appropriate interval. For example, S_{spawn} for cutthroat trout (i.e., over the 275-d interval) was estimated as $0.356^{(275/365)} = 0.459$, where 0.356 is the annual survival rate for large adults (Table 1). The S_{egg} for cutthroat trout (Table 1) over 90 d was similarly estimated as 0.400 based on the egg to age-1 survival rate of 0.02647 for Yellowstone cutthroat trout

O. clarkii bouvieri (Stapp and Hayward 2002). This estimate is similar to the product of egg to hatch success (Ball and Cope 1961; Mills 1966) and hatchling to winter survival (~ 0.50 – 0.75) for Colorado River cutthroat trout reared in natural temperature regimes with a 10°C average summer temperature (Coleman and Fausch 2007).

Deterministic brook trout matrix model.—A four-stage model for brook trout (Figure 1B; Table 1) was based on demographic data from the control streams of Peterson et al. (2004). Survival rates for age-0 and older brook trout were calculated as the mean for 2 years (1998 and 1999; Appendix B in Peterson et al. 2004). Estimates from 2000 were excluded from the matrix model values because they might have been influenced by very high brook trout density, and we wanted the brook trout model to represent high growth potential. We account for density dependence elsewhere (as described below in *Density dependence*). Egg to age-0 survival over a 1-year period from fall spawning to census during the subsequent fall (S_{egg} for brook trout; Table 1) was estimated as the midpoint of the mean and high values used in the models of Adams (1999; based on data from McFadden et al. 1967) and is similar to the range of values reported for the whitespotted char *S. leucomaenis* (e.g., Morita and Yokota 2002).

The F for brook trout was defined the same as that for cutthroat trout but was calculated (1) using different maturity and fecundity schedules and (2) without a term for adult survival, because the dates of census and spawning were close (Table 1). Length at first maturity and the proportion of females that were mature in the three oldest stages were based on the logistic regression equation of Kennedy et al. (2003) from two of the streams studied by Peterson et al. (2004; Table 1). The length-classes of adult brook trout encompassed the range of sizes encountered for age-2 and older individuals in study streams (Peterson and Fausch 2002). We divided adults into two size categories (small: ≤ 170 mm FL; large: > 170 mm FL) that were based approximately on the mean length of age-2 and older brook trout in the mid-elevation treatment stream prior to the experimental suppression (Table 4 in Peterson et al. 2004). Fecundity was estimated using a length–fecundity relationship from a composite sample of brook trout collected at nine streams in Alberta, Canada (number of eggs per female = $[7 \times \text{FL}] - 819$, where FL is in mm; Tripp et al. 1979). Stream-resident cutthroat trout in the western USA generally have low numbers of eggs (~ 200 – 400 eggs/female; e.g., Quinlan 1980; Downs et al. 1997; Pritchard and Cowley 2006; M. Japhet, Colorado Division of Wildlife, unpublished data), whereas brook trout fecundity

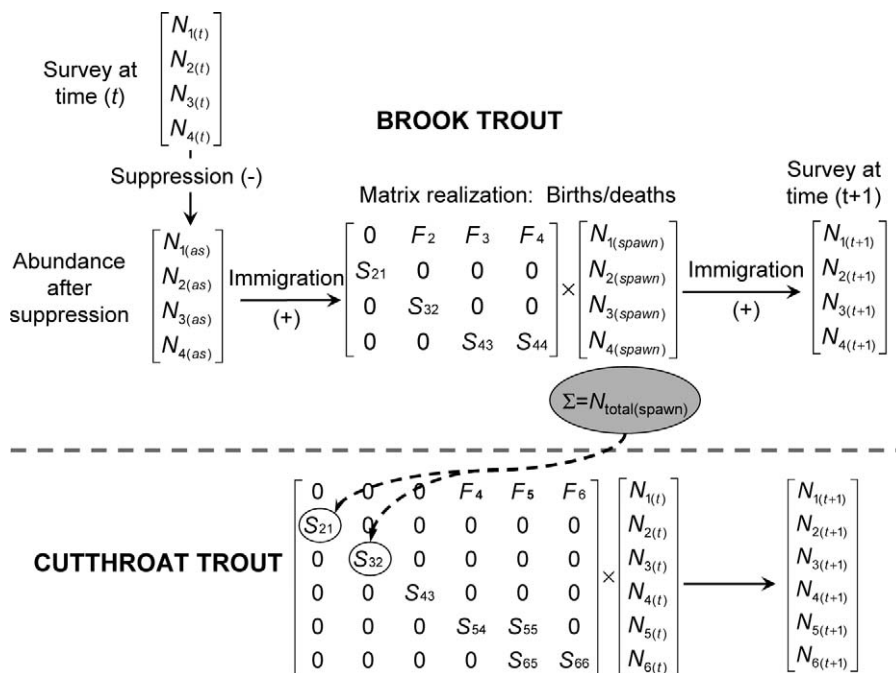


FIGURE 2.—Matrix representations of the population ecology of native cutthroat trout and nonnative brook trout, where brook trout are subjected to electrofishing suppression across one time step (i.e., from time t to $t + 1$). The number of brook trout remaining in each stage (i) after electrofishing suppression, $N_{i(as)}$, and the number of immigrants arriving after the fall suppression event are summed to obtain the stage-specific brook trout population size at fall spawning, $N_{i(spawn)}$. The sum of $N_{i(spawn)}$ for all brook trout stages, $N_{total(spawn)}$, represents the strength of competition and predation effects on cutthroat trout. Brook trout abundance in the next time step ($t + 1$) is the sum of the matrix projection for the population at spawning plus the number of postspawning immigrants during winter through summer, $N_{i(t+1)}$. For cutthroat trout, the system is closed to immigration and the survival rates of age-0 and age-1 fish are influenced by brook trout abundance (dashed arrows). Table 1 defines additional matrix parameter notations and values.

appears to be greater than that of cutthroat trout at a given length (Adams 1999; Young 2008). Consequently, in our models, brook trout have greater length-specific fecundity than do cutthroat trout. We refer to age 1 as a subadult stage, because most females are not mature and the overall F of that stage is negligible (Table 1).

Model Simulations

Linking the demography of brook trout and cutthroat trout.—Our approach was to link the demographic models for brook trout and cutthroat trout to mimic the biotic interactions (competition and predation; e.g., Novinger 2000) that reduce the survival of young cutthroat trout when the two species are sympatric. We manipulated the strength of these biotic interactions by considering brook trout suppression in the model. Electrofishing suppression is conducted in the fall, when streams are at base flow and all age-classes of both species are available for capture. We wanted trout demography in the model to represent

conditions in the mid-elevation streams of Peterson and Fausch (2003b) and Peterson et al. (2004). We assumed that (1) cutthroat trout populations are demographically closed because they are isolated in headwater streams by nonnative trout invasions (Peterson and Fausch 2003a, 2003b; Peterson et al. 2004); (2) brook trout populations are demographically open, often having source populations downstream (Peterson and Fausch 2003b); (3) brook trout immigrants arrive in both fall (after electrofishing suppression) and spring (Peterson and Fausch 2003b); and (4) brook trout immigrating in the fall are mature adults that successfully spawn.

The population ecology of brook trout under suppression and the linkage to cutthroat trout are depicted in Figure 2. Briefly, electrofishing suppression conducted in the late summer or early fall removes a proportion of the brook trout population. Brook trout abundance after suppression can be supplemented by immigrants that arrive after the suppression event but before spawning. Brook trout abundance at spawning

($N_{\text{total}(\text{spawn})}$) is the value that influences the vital rates of young cutthroat trout (see below). The stage-specific composition of $N_{i(\text{spawn})}$ is multiplied by the vital rates in the matrix to project brook trout abundance into the next time step. Adult brook trout can also immigrate into the stream segment in winter through early summer after the birth pulse.

Cutthroat trout abundance through time was a function of the current abundance and the vital rates in the matrix model, which varied with brook trout density (Figure 2). We found no empirical evidence that brook trout affected the survival of adult Colorado River cutthroat trout (Peterson et al. 2004), so adult vital rates did not vary relative to brook trout. In contrast, S_{21} and S_{32} for cutthroat trout were strongly reduced by brook trout (Shepard et al. 2002; Peterson et al. 2004), so we varied these vital rates using a modified type III functional response equation:

$$S_{21} \text{ or } S_{32} = \frac{(D^m S_{\text{high}}) + \{[N_{\text{total}(\text{spawn})}]^m S_{\text{low}}\}}{D^m [N_{\text{total}(\text{spawn})}]^m},$$

where D is the inflection point for the functional response ($D = 500$); m is a parameter that influences the shape of the curve ($m = 5$); $N_{\text{total}(\text{spawn})}$ is brook trout abundance at fall spawning (Figure 2), which corresponds to the brook trout abundance at the beginning of the interval over which cutthroat trout survival estimates were measured (Peterson et al. 2004); S_{high} is the stage-specific survival rate for age-0 or juvenile cutthroat trout under conditions of constant brook trout suppression; and S_{low} is the stage-specific survival rate for age-0 or juvenile cutthroat trout under conditions of no brook trout suppression (Table 1).

The values of D and m were selected to produce the nonlinear relationship found between brook trout density and the survival of age-1 and younger cutthroat trout. The functional response equation plotted across a range of brook trout densities (x -axis) appears as a logistic curve bounded by the high and low values (y -axis) of S_{21} or S_{32} (Table 1), and the inflection point (where survival declines sharply) occurs at a brook trout abundance of 250–500 fish/km (Figure 4 in Peterson et al. 2004).

Spatial and temporal boundaries of the model.—Simulations were for annual time steps over a total period of 50 years and assumed sympatric populations in a 1-km stream segment. Fifty years was chosen to represent a balance between the maximum foreseeable future for resource management or conservation plans and a sufficiently long time period over which population projections exhibit characteristic behavior given the life history of the species. In this case, 50

years encompassed at least nine generations for both brook trout and cutthroat trout (estimated at 3.9 and 5.0–5.5 years/generation, respectively, from the deterministic matrices; Figure 1; Table 1).

Populations of cutthroat trout in the interior western USA often exist as small, isolated resident populations in stream segments of a few kilometers or less (e.g., Harig and Fausch 2002; Shepard et al. 2005; Young et al. 2005; Young 2008). A 1-km stream segment is also the approximate spatial extent of the field experiment that provided the empirical data for the models. We expect that estimates of population growth derived from the models are scalable to other short segments of headwater streams for which the conditions hold.

Density dependence.—The potential for density-dependent processes to influence simulated cutthroat trout population response was considered in two ways. First, we placed an upper limit on age-0 recruitment for both species (500) to represent density dependence in early life history. Second, because brook trout appear to be capable of high population growth rates (λ ; e.g., Peterson et al. 2004), each matrix element was scaled by

$$\frac{1}{\left\{1 + \left[\frac{\lambda_{\text{BKT}} - 1}{1,000}\right] N_{\text{total}(\text{spawn})}\right\}}$$

(Poole 1974; Hilderbrand 2003), which reduces F and survival of brook trout as abundance increases. In the scaling factor, λ_{BKT} is the dominant eigenvalue of the brook trout matrix (i.e., population growth rate), $N_{\text{total}(\text{spawn})}$ is the current abundance of brook trout, and 1,000 represents the total carrying capacity of brook trout. We did not include a similar term for cutthroat trout because we assumed that the biotic effects of sympatry with brook trout would keep cutthroat trout abundance below the level at which intraspecific competition would lead to density dependence.

Stochasticity.—Temporal variation in survival rates for both species was included by randomly selecting values from a beta distribution (between 0 and 1; e.g., Morris and Doak 2002) using the mean estimated values from Table 1. We assumed that S_{21} and S_{32} for both species exhibited greater temporal variation (SD based on coefficient of variation [CV] = 20%) than the survival rates for older age-classes (10%). The standard errors of Colorado River cutthroat trout vital rates reported by Peterson et al. (2004) did not decompose sampling and process variance, and we considered the variation (i.e., CV) used in this modeling exercise to include both parameter uncertainty and temporal environmental variation (stochasticity). The model and simulations assumed no correlation among vital rates, such as that caused by catastrophes. Demograph-

TABLE 2.—Stage-specific brook trout removal efficiency for one- and two-pass electrofishing modeled under high and low capture probabilities, and maximum brook trout immigration rates (fish/year) used in simulations for examining the effect of nonnative brook trout (and their suppression) on native cutthroat trout populations. The relative proportion of brook trout immigrants at each time and life stage remained the same for reduced immigration rates.

Life stage	High capture probability		Low capture probability		Maximum immigration rate by season	
	One-pass efficiency ^a	Two-pass efficiency	One-pass efficiency	Two-pass efficiency ^b	Fall	Early summer
Age 0	0.60	0.84	0.45	0.70	-	-
Age 1	0.70	0.91	0.50	0.75	-	-
Small adult	0.75	0.94	0.55	0.80	25	25
Large adult	0.75	0.94	0.55	0.80	25	25

^a Removal efficiency is defined as the proportion of brook trout that are captured and removed during one electrofishing pass. Two-pass efficiency was calculated using constant one-pass capture probabilities.
^b Simulations were not conducted for two-pass suppression under low capture probability because removal efficiencies were similar to those of one-pass suppression under high capture probability (only 6–16% greater) and simulation results would have been qualitatively similar.

ic stochasticity was not explicitly considered in our model projections because we used a quasi-extinction threshold (50 individuals; see *Analyses*) above which this phenomenon is probably negligible (Morris and Doak 2002).

Initial conditions.—The starting population size for both species was 500 fish. Preliminary sensitivity analyses indicated that modeling results were relatively insensitive to starting population sizes across a range of 250–1,000. Initial stage-specific abundances (N_i) of brook trout were 200 age-0 fish, 100 subadults, 100 small adults, and 100 large adults. Cutthroat trout abundances were 200 age-0 fish, 100 juveniles, and 50 fish in each of the remaining four stages. The default brook trout immigration rate of 100 fish/year (Table 2) was based on the high immigration rates measured in a mid-elevation stream in the experiment by Peterson and Fausch (2003b) and was consistent with the ability of brook trout to rapidly recolonize stream reaches

from a source population after suppression (Peterson et al. 2004; Meyer et al. 2006) or disturbance (Roghair and Dolloff 2005).

Brook Trout Suppression Scenarios

Our objective was to analyze maintenance control of brook trout and the resulting population response of cutthroat trout across various plausible levels of electrofishing frequency, electrofishing intensity, capture efficiency, and brook trout immigration rate. Brook trout abundance was modeled as a function of (1) electrofishing frequency, defined as the frequency of annual suppression visits over 50 years; (2) the temporal distribution of suppression visits; and (3) intensity, defined as the number of electrofishing passes per suppression visit. We did not analyze three or more electrofishing passes because we assumed that the ideal goal of eradication was not possible because of logistical or financial constraints.

Accordingly, we selected three suppression visit frequencies (20, 25, and 30 visits over 50 years) and generated systematic patterns of temporal distribution of suppression events (labeled A–C) for each frequency (Table 3). We modeled both one- and two-pass electrofishing and set the capture probability (removal efficiency per pass) to at least 0.6 for each brook trout stage (Table 2; Peterson et al. 2004). This combination of suppression visit frequency (3 levels), temporal distribution of suppression (3 per frequency), and suppression intensity per visit (2 levels) yielded a set of 18 initial scenarios that assumed 100 brook trout immigrants/year. We also modeled scenarios of annual suppression and no suppression to understand the boundaries of cutthroat trout population response.

Suppression scenarios that showed significant promise to help cutthroat trout persist in sympatry with brook trout were further evaluated using lower capture

TABLE 3.—Brook trout electrofishing suppression scenarios used in simulations for examining the effect of nonnative brook trout on native cutthroat trout populations. Temporal distribution codes A–C designate the systematic, repeated patterns of electrofishing visits under a given frequency of suppression (20, 25, or 30 visits over a total period of 50 years). For example, 20A represents two consecutive years of suppression (2 years on) followed by 3 years of no suppression (3 years off), and repetition of this 5-year cycle results in 20 visits over 50 years.

Temporal distribution code	Number of suppression visits over 50 years		
	20	25	30
A	2 on, 3 off	1 on, 1 off	3 on, 2 off
B	4 on, 6 off	2 on, 2 off	4 on, 2 off, 2 on, 2 off
C	1 on, 1 off, 1 on, 2 off	3 on, 3 off	6 on, 4 off

probabilities to represent suppression in larger streams or those with more-complex habitat (Table 2). These scenarios were also modeled across a range of reduced rates of brook trout immigration (0, 25, 50, and 75 fish/year).

Multiple-pass electrofishing can injure individual trout and, when combined with handling stress, can cause mortality. Despite this, population-level declines have not been detected when resident trout were repeatedly electrofished over 4–12 consecutive years (Habera et al. 1996; Kocovsky et al. 1997; Carline 2001; Peterson et al. 2004). Because the Colorado River cutthroat trout survival estimates of Peterson et al. (2004) already account for any chronic effects of electrofishing and because population-level data for trout indicate that natural mortality rates are partly compensatory, we decided not to formally account for electrofishing and handling effects in our model.

Analyses

To understand how changes in specific vital rates can affect deterministic population growth (λ) for each species, we estimated the sensitivity of λ to absolute changes (sensitivity) and proportional changes (elasticity) in each matrix element (Morris and Doak 2002). We quantified cutthroat trout population response in stochastic simulations using three metrics: (1) λ , (2) frequency of extinction, and (3) median time to extinction. Persistence was defined as maintaining a total population size greater than 50; cutthroat trout populations were considered extinct and simulations ended if the total population size dropped below this quasi-extinction threshold at any time. All stochastic simulations were iterated 1,000 times using MATLAB version 6.5 (MathWorks, Inc.), and summary statistics for cutthroat trout population response were calculated using the Statistical Analysis System version 9.0 (SAS Institute, Inc.). We used the median value as the summary statistic for both λ and time to extinction, and we calculated empirical cumulative distribution functions (CDFs) to depict extinction probability through time (e.g., Morris and Doak 2002).

Benefit–Cost Analysis

To evaluate the relative performance of suppression treatments given the resource limitations faced by state and federal agencies that manage cutthroat trout, we conducted a post hoc cost–benefit analysis of selected suppression scenarios. We calculated benefit–cost ratios for selected scenarios based on the increase in λ for cutthroat trout and compared estimates across three levels of brook trout immigration (25, 50, and 100 fish/year) and crew travel time (4, 12, and 24 h) to and from the stream. The analysis assumed a 3-km

stream segment. Estimates of λ from the 1-km modeling frame were scaled up to 3 km because this is more typical of the stream length at which biologists would implement suppression efforts (Shepard and Nelson 2004). The λ as estimated by the model is largely independent of spatial scale, so results should be applicable to segments of varying length in small, headwater streams (e.g., Peterson et al. 2004; Young et al. 2005). In contrast, because of uncertain scalability, we did not include a cost–benefit example for persistence, which is a binary response based on an arbitrary threshold. The analysis further assumed that crews require 45 min to complete one-pass electrofishing and 75 min to complete two-pass electrofishing in 100 m of stream habitat. Electrofishing times approximated those recorded in the four Colorado streams by Peterson et al. (2004; electrofishing rates: D.P.P and K.D.F., unpublished data) and were similar to those reported for brook trout suppression efforts in other Rocky Mountain streams (K. Rogers, Colorado Division of Wildlife, personal communication; M. Enk, U.S. Forest Service, personal communication).

Benefit–cost ratios were calculated using effect size divided by time (cost) as

$$\frac{\lambda_{\text{suppr}} - \lambda_{\text{nosuppr}}}{\left[\frac{(\text{freq visits})(\text{time}_{\text{ele}} + \text{time}_{\text{trv}})}{50} \right]},$$

where λ_{suppr} is the median value of λ with suppression; λ_{nosuppr} is the median without suppression; frequency of visits is 20, 25, or 30; electrofishing time is given in hours; travel time is the number of hours required to transport the crew to and from the site; and 50 represents the period of evaluation (years). Three levels of travel time (4, 12, and 24 h) were selected to represent sites ranging from accessible to remote. We assumed that field gear preparation was a fixed cost, and we did not include it in the calculation. The benefit–cost ratios give the increase in λ per unit time (h/year) averaged over 50 years.

Results

Deterministic Matrix Models: General Characteristics and Sensitivities

In the absence of density dependence and variation in vital rates, cutthroat trout populations subjected to very strong biotic effects from brook trout decreased by 39% per year ($\lambda = 0.61$) based on the model, while populations for which biotic effects from brook trout were negligible (i.e., suppression) increased by 10% per year ($\lambda = 1.10$). These estimates depended on whether S_{21} and S_{32} were either both low or both high, respectively (Table 1). For brook trout, the demo-

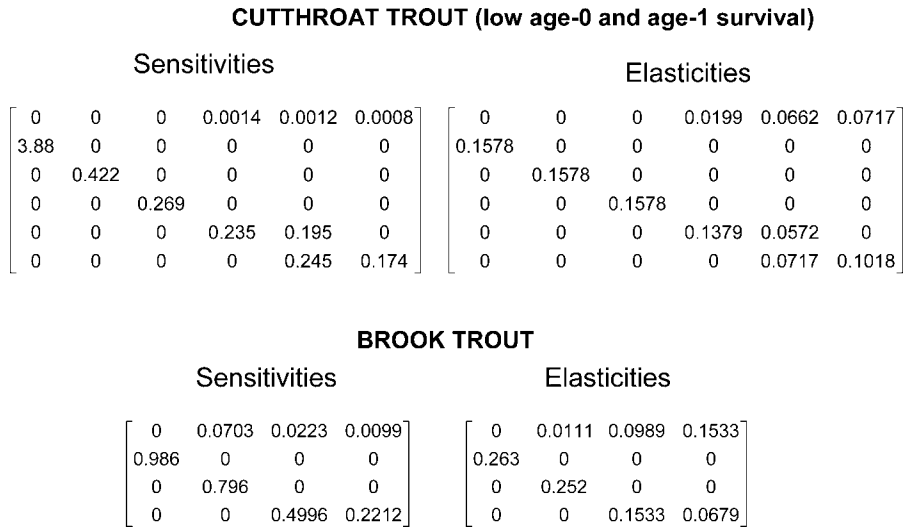


FIGURE 3.—Responses of population growth rate (λ) to absolute (sensitivity) and proportional (elasticity) changes in matrix elements (Table 1; Figure 1) for deterministic models of native cutthroat trout and nonnative brook trout populations. Values for cutthroat trout were calculated using the low age-0 and age-1 survival estimates to represent a strong biotic effect from brook trout. Elasticity values sum to 1.0 for a given matrix (Morris and Doak 2002).

graphic model predicted a 20% increase per year ($\lambda = 1.20$) in the absence of density dependence.

The λ -values for both species were particularly sensitive to changes in S_{21} and S_{32} but were less sensitive to changes in adult survival rates and also comparatively insensitive to changes in F (Figure 3). When biotic effects from brook trout were strong, the cutthroat trout λ was at least 8–10 times more sensitive to absolute changes in S_{21} than other matrix elements and was also most elastic in response to proportional changes in survival during the first 3 years of life (Figure 3). The brook trout λ also exhibited the greatest sensitivity and elasticity to S_{21} and S_{32} . Therefore, from the deterministic model, management actions that increase the survival rates of young cutthroat trout can be inferred to have the greatest potential for improving the population status of cutthroat trout. We caution, however, that population response in the cutthroat trout model is not insensitive to survival of age-2 and older individuals, because that particular vital rate is represented by multiple individual matrix entries (e.g., S_{43} , S_{54} , S_{55} , S_{65} , and S_{66} for cutthroat trout) and is included in the formula for F .

Stochastic Simulations: Cutthroat Trout Response to Brook Trout and Suppression

Under initial conditions of very high brook trout immigration (100 fish/year), no brook trout suppression, and variation in vital rates, the cutthroat trout population decline was precipitous (30% per year) and populations

went extinct (i.e., fell below the quasi-extinction threshold) at a median time of 10 years (Table 4; Figure 4). In contrast, when brook trout were suppressed each year and when capture probabilities were high, the cutthroat trout populations increased ($\lambda = 1.008$) to a carrying capacity of approximately 700 individuals and persisted indefinitely. Other suppression treatments created cyclic oscillations in cutthroat trout abundance (Figure 4) that were driven by changes in S_{21} and S_{32} and depended on the temporal distribution of suppression visits. For example, scenario 20A, which involved two consecutive years of suppression followed by 3 years without suppression (2 years on, 3 years off), created a cycle with low abundance every 5 years; scenario 25B (2 years on, 2 years off) produced a cycle with low abundance every 4 years.

Suppression frequency.—Relative to the no-suppression scenario, simulated cutthroat trout populations responded positively to electrofishing suppression of brook trout across the range of modeled scenarios under an assumption of high brook trout capture probability (Table 4; Figures 4, 5). Not surprisingly, the magnitude of the response increased with the frequency of suppression. As the frequency increased from 20 to 30 visits over 50 years, cutthroat trout populations declined more slowly and were less likely to go extinct, but they never grew. For example, as the frequency increased from 20 to 25 or 30 visits, the median λ increased from 0.875 to 0.909 or 0.95 and the median time to extinction increased from 20 to 27.3 or

TABLE 4.—Cutthroat trout population responses to various scenarios (Table 3) of nonnative brook trout suppression with one- or two-pass electrofishing; responses are median (\pm 95th percentile and SD) population growth rate (λ), frequency of extinction at 20 or 50 years, and median number of years to extinction. Values are based on 1,000 stochastic iterations of each scenario for a simulation period of 50 years; brook trout were assumed to have a high capture probability and an immigration rate of 100 fish/year. Extinction was defined as falling below the quasi-extinction threshold of 50 fish.

Scenario	Passes	λ^a		Extinction frequency		Years to extinction	
		Median ^b (95th percentile)	SD			Median ^c (95th percentile)	SD
				20 years	50 years		
No suppression	-	0.69 (0.679–0.702)	0.007	1,000	1,000	10 (7–12)	0.739
20A	1	0.915 (0.892–0.938)	0.014	217	997	23 (18–38)	6.0
	2	0.936 (0.913–0.958)	0.014	51	909	33 (18–48)	7.91
20B	1	0.835 (0.82–0.851)	0.009	1,000	1,000	18 (15–19)	1.35
	2	0.847 (0.831–0.862)	0.009	993	1,000	19 (17–20)	1.06
20C	1	0.875 (0.857–0.895)	0.011	696	1,000	19 (15–24)	2.52
	2	0.905 (0.886–0.926)	0.012	152	1,000	24 (19–32)	3.82
25A	1	0.898 (0.882–0.915)	0.010	123	1,000	24 (20–30)	3.41
	2	0.930 (0.913–0.949)	0.011	3	992	34 (25–44)	5.69
25B	1	0.912 (0.892–0.932)	0.012	77	1,000	27 (20–35)	4.68
	2	0.934 (0.915–0.954)	0.012	6	967	35 (24–44)	6.07
25C	1	0.916 (0.90–0.935)	0.011	6	1,000	31 (21–39)	5.1
	2	0.934 (0.915–0.953)	0.011	0	975	38 (27–50)	6.5
30A	1	0.963 (0.932–0.989)	0.017	0	107	44 (34–49)	5.43
	2	0.987 (0.970–0.999)	0.009	0	3	-	2.9
30B	1	0.955 (0.935–0.974)	0.012	0	509	40 (29–49)	6.52
	2	0.972 (0.953–0.986)	0.010	0	68	49 (29–50)	6.47
30C	1	0.932 (0.914–0.954)	0.012	1	993	32 (23–42)	5.20
	2	0.950 (0.930–0.970)	0.013	0	864	33 (29–43)	5.78
Annual suppression	1	1.008 (1.004–1.009)	0.002	0	0	-	-
	2	1.008 (1.005–1.01)	0.001	0	0	-	-

^a Summary statistics for cutthroat trout λ were calculated at the end of the 50-year projection or in the year of lowest abundance closest to year 50, based on visual inspection of abundance averaged over the 1,000 iterations. This adjustment accounted for the different population cycles imposed by the suppression scenarios (e.g., see Figure 4). The λ was generally calculated based on abundances in year 50, but exceptions were 20A and 25B (both year 49) and 30A and 30B (both year 48).

^b Median and mean values were equal to at least two decimal places.

^c Median time to extinction was calculated based on only those iterations in which cutthroat trout went extinct within 50 years and only for those scenarios in which extinction occurred for at least 5% of simulations (50).

38.6 years (values averaged for one-pass electrofishing for a given frequency; Table 4).

Temporal distribution of suppression.—The temporal distribution of suppression events strongly influenced cutthroat trout population response for a given frequency of suppression. Generally, the strongest positive response was observed when at least two consecutive years of suppression were used in combination with no more than 3 years without suppression (Table 4; Figure 5). Differences in λ among suppression scenarios were most pronounced for 20 and 30 visits; scenarios 20A (2 years on, 3 years off) and 30A (3 years on, 2 years off) produced the strongest responses in their respective categories, whereas scenarios with fewer consecutive years of suppression (20C) or longer periods without suppression (20B and 30C) performed less well. Suppression scenarios 25B (2 years on, 2 years off) and 25C (3 years on, 3 years off) produced similar values of λ (0.912 and 0.916, respectively, for one-pass suppression).

Extinction frequency and the temporal progression of extinction events showed similar patterns; scenarios

20A, 25B, 25C, and 30A produced the most favorable cutthroat trout response within each category (Table 4; Figure 5). Among scenarios involving 20 suppression visits and one-pass electrofishing, scenario 20A resulted in the highest probability of population persistence for 20 years (0.783 versus 0.000 for 20B and 0.304 for 20C). The probability of extinction under 20A increased significantly after year 17 (i.e., CDF rose sharply; Figure 5), whereas the increase happened earlier or was more pronounced for scenarios 20B and 20C. Among scenarios with 25 suppression visits and one-pass electrofishing, scenarios 25B and 25C produced the highest probabilities of population persistence for 20 years (>0.923 versus 0.877 for 25A), and extinction probabilities did not increase dramatically until after year 20 (Figure 4). Among scenarios with 30 suppression visits and one-pass electrofishing, scenario 30A resulted in the highest probability of population persistence for 50 years (0.893) and few populations went extinct. In contrast and despite the same overall frequency of suppression, cutthroat trout populations modeled under scenarios

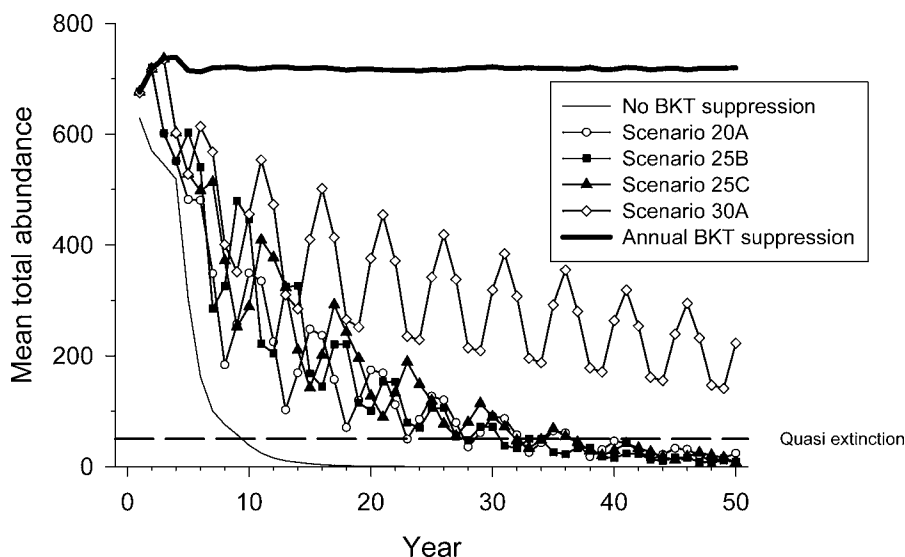


FIGURE 4.—Abundance of native cutthroat trout under nonnative brook trout (BKT) suppression scenarios of different frequency (scenarios defined in Table 3) given assumptions of one-pass electrofishing, a high capture probability, and a BKT immigration rate of 100 fish/year. Each point represents mean total abundance at each time step across 1,000 simulations; the horizontal line at 50 represents the quasi-extinction threshold for cutthroat trout.

30B and 30C were much more likely to go extinct within 50 years (probability of persistence = 0.491 and 0.007, respectively) and to do so sooner (median time to extinction was 4–12 years earlier; Table 4) than populations modeled under scenario 30A.

Suppression intensity.—Increasing the intensity of a given suppression event by changing from one- to two-pass electrofishing improved measures of cutthroat trout population viability for most scenarios (Table 4; Figure 5), because a higher proportion of the brook trout population was removed (Table 2). Increases in λ and time to extinction varied by frequency of suppression and by the temporal distribution of visits within each frequency, but use of the second electrofishing pass obtained an overall mean increase of 0.0216 in λ and a mean increase of 6.3 years in median time to extinction (Table 4). The exception was annual suppression, for which a second electrofishing pass under high capture probabilities did not yield any additional benefit. The results provided a basis to compare scenarios of lower-frequency, higher-intensity suppression with scenarios of higher-frequency, lower-intensity suppression; for example, such a comparison is useful if there are concerns that repeated electrofishing could affect cutthroat trout behavior, growth, and survival. Over a 10-year period, implementation of scenarios 20A (two passes) and 30A (one pass) would subject the cutthroat trout population to eight and six total electrofishing runs, respectively, yet the latter

scenario is expected to produce more-robust cutthroat trout populations.

Effects of Reduced Capture Probability and Immigration by Brook Trout for Best-Performing Scenarios

On the basis of the preceding results, we selected 20A, 25B, 25C, and 30A as the best-performing scenarios for a given frequency of suppression and used them to explore the effects of reduced electrofishing capture probability and brook trout immigration. A decrease in capture probability reduced all measures of cutthroat trout population viability for a given suppression scenario (Table 5; Figure 6). A decrease in the annual number of brook trout immigrants increased both λ and time to extinction, but the rates of increase in these metrics suggested the presence of a threshold immigration value that depended on both suppression frequency and capture probability. At the highest immigration rate and with one-pass suppression, λ declined by about 0.05 and the median time to extinction decreased by 5–16 years across scenarios when capture probability decreased. However, these differences diminished as brook trout immigration declined.

Under conditions of low capture probability and one-pass suppression in all scenarios, the sharpest increases in cutthroat trout viability metrics occurred as brook trout immigration dropped to 25 fish/year or less:

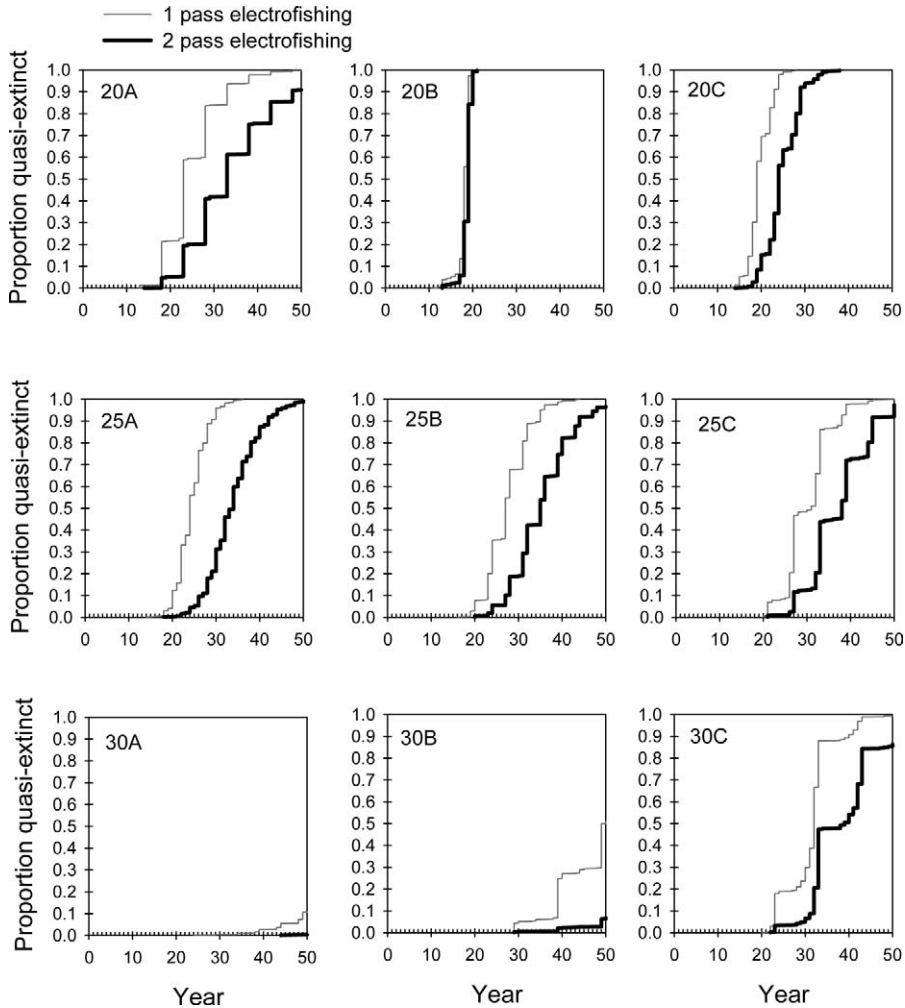


FIGURE 5.—Empirical cumulative distribution functions (CDFs) illustrating native cutthroat trout quasi-extinction (i.e., a population falling below a threshold of 50 fish) under different nonnative brook trout suppression scenarios (defined in Table 3) and electrofishing intensities (1–2 passes). Plots represent the proportion of 1,000 simulations in which the cutthroat trout population went extinct by a given year under assumptions of high capture probability and a brook trout immigration rate of 100 fish/year.

median time to extinction increased by at least 12 years and λ increased by at least 0.04 (Table 5; Figure 6). For the scenario of highest suppression frequency (30A), cutthroat trout population response varied little with a reduction in capture probability when brook trout immigration was 25 fish/year or less. In contrast, all other scenarios were only robust to capture probability reduction if brook trout immigration was zero. Similarly, for all four scenarios, little additional benefit was gained by use of a second electrofishing pass when capture probability was high and when brook trout immigration was 25 fish/year or less.

Benefit–Cost Analysis for Best-Performing Scenarios

Benefit–cost analysis of λ indicated that low-frequency, one-pass electrofishing suppression was the most cost effective or as cost effective as all other scenarios under modeled conditions (Figure 7). When travel time was minimal (4 h) and when capture efficiency was high (>0.60), then the greatest benefit–cost ratio was obtained for lower-frequency (20A), one-pass electrofishing over all levels of brook trout immigration. The same was true when capture probability was low; however, the benefit–cost ratio was lower than that obtained under the high capture probability. The benefit–cost ratio of the lower-

TABLE 5.—Frequency of cutthroat trout quasi-extinction (number of simulations in which the population fell below a threshold of 50 fish) and median (\pm 95th percentile) time to extinction (years) under selected scenarios (Table 3) of nonnative brook trout suppression with one- or two-pass electrofishing, high or low capture efficiency, and various brook trout immigration rates (0–100 fish/year). Values are based on 1,000 stochastic iterations of each scenario for a simulation period of 50 years.

Scenario	Passes	Capture probability ^a	Quasi-extinction at 50 years by brook trout immigration rate					Median time to extinction (95th percentile) ^b by brook trout immigration rate				
			100	75	50	25	0	100	75	50	25	0
20A	1	High	997	984	810	5	0	23 (18–38)	28 (18–43)	34 (23–48)	-	-
	2	High	909	649	80	0	0	33 (18–48)	38 (23–48)	43 (33–49)	-	-
25B	1	Low	1,000	1,000	1,000	963	0	18 (13–18)	18 (13–23)	18 (17–28)	33 (23–44)	-
	1	High	1,000	1,000	757	0	0	27 (20–35)	31 (23–40)	40 (28–48)	-	-
25C	2	High	990	682	8	0	0	35 (24–44)	40 (31–48)	-	-	-
	1	Low	1,000	1,000	1,000	743	0	19 (15–23)	20 (16–24)	23 (19–28)	40 (28–48)	-
30A	1	High	1,000	996	846	1	0	31 (21–39)	33 (26–45)	39 (28–50)	-	-
	2	High	975	817	125	0	0	38 (27–50)	39 (32–50)	45 (38–50)	-	-
All	1	Low	1,000	1,000	1,000	754	0	20 (15–26)	21 (18–27)	26 (20–32)	43 (32–50)	-
	1	High	107	43	3	0	0	44 (34–49)	-	-	-	-
	2	High	3	0	0	0	0	-	-	-	-	-
	1	Low	1,000	985	805	0	0	28 (19–37)	33 (23–44)	38 (28–49)	-	-
	1	High	0	0	0	0	0	-	-	-	-	-
	2	High	0	0	0	0	0	-	-	-	-	-
	1	Low	0	0	0	0	0	-	-	-	-	-

^a We did not directly model two-pass electrofishing under low capture probability because the suppression effect would be roughly equivalent to that of one-pass electrofishing under high capture probability for a given scenario (see Table 2).

^b Median time to extinction was calculated based on only those iterations in which cutthroat trout went extinct within 50 years and only for those scenarios in which extinction occurred for at least 5% of simulations.

frequency scenario increased as brook trout immigration decreased. As travel time increased to 12 or 24 h, the lower-frequency, one-pass scenario was still best (or was never worse than two-pass suppression or any other scenario), but the differences among scenarios and suppression intensity levels became very small. Therefore, in terms of obtaining increases in λ , there was no benefit–cost justification for a second electrofishing pass. However, the most cost-effective scenario led to a stable population ($\lambda \approx 1.0$) only when brook trout immigration was 25 fish/year or lower (Figures 6, 7).

Discussion

Mechanisms of Displacement and Response to Electrofishing Suppression

The matrix models we constructed to depict the population ecology of brook trout and cutthroat trout and their responses to brook trout suppression appeared to capture the important dynamics of these species in small, headwater Rocky Mountain streams. The values of λ estimated from the deterministic matrices were consistent with empirical estimates for these species from a manipulative field experiment (Peterson et al. 2004). For example, the geometric mean λ of Colorado River cutthroat trout in lower-elevation streams based on removal estimates of abundance was 1.08 in areas where brook trout were suppressed and 0.58 in areas where suppression was not conducted (Appendix B in Peterson et al. 2004). These λ -values agreed closely

with the model-based predictions of 1.10 and 0.61, respectively. Empirical and model evidence also demonstrated that brook trout are capable of rapid population growth. The λ measured for brook trout in the low-elevation control stream of Peterson et al. (2004) was 1.34, whereas the model estimate was 1.20. Likewise, modeled λ -values for brook trout in a productive Montana stream were high (1.14–1.29; Adams 1999).

Our models (1) highlight the demographic advantage of brook trout in sympatry with resident cutthroat trout and (2) strengthen the conclusion that recruitment bottlenecks associated with reduced survival of young cutthroat trout constitute a mechanism by which brook trout displace cutthroat trout (Peterson et al. 2004; McGrath and Lewis 2007). The faster individual growth, earlier maturity (Kennedy et al. 2003; Paul et al. 2003), and greater fecundity (Downs et al. 1997; Adams 1999; Young 2008) of brook trout impart a distinct demographic advantage over cutthroat trout (Dunham et al. 2002). Based on the model, annual λ was 10% greater for brook trout in sympatry (1.20) than for cutthroat trout in allopatry (1.10). However, brook trout invasion produced lower survival of cutthroat trout young, causing cutthroat trout λ to be half of the brook trout λ and pushing cutthroat trout populations into a strong decline. This demographic asymmetry resulted in extirpation and displacement of cutthroat trout in about 10 years during model simulations; this finding is consistent with observations

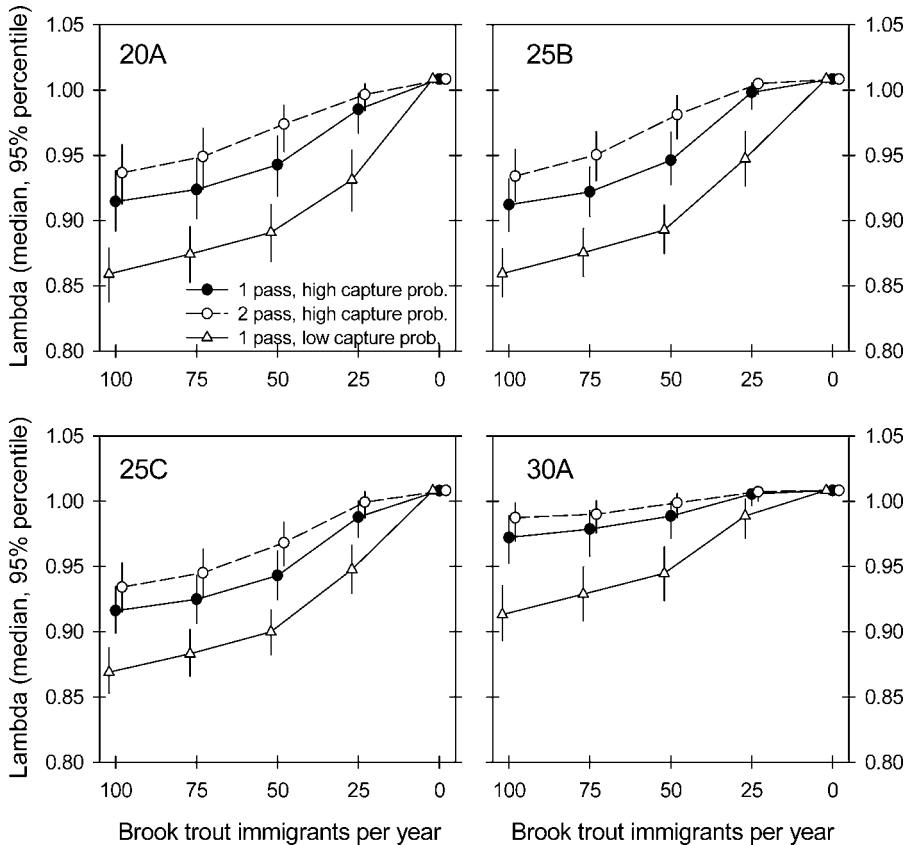


FIGURE 6.—Median (\pm 95th percentile) population growth rate (λ) of native cutthroat trout under selected nonnative brook trout suppression scenarios (defined in Table 3) given different levels of electrofishing intensity (1–2 passes), capture probability (high or low), and brook trout immigration rate (0–100 fish/year).

from wild populations of several cutthroat trout subspecies in different regions (e.g., Behnke 1992; Rosenlund et al. 2001; A. Harper, U.S. Forest Service, personal communication). Population models often indicate that population growth in stream-resident trout is sensitive to changes in juvenile survival (Hilderbrand 2003; Veléz-Espino et al. 2006). Both demographic and individual-based models indicate that nonhybridizing, invasive trout can limit populations of native salmonids by reducing juvenile survival (Clark and Rose 1997; Stapp and Hayward 2002). Rapid displacement of inland cutthroat trout may not always occur after invasion by brook trout (Adams et al. 2002; Dunham et al. 2002), but the threat of displacement often puts pressure on biologists to act, even if only to use electrofishing suppression as a temporary measure to slow extirpation.

Our model demonstrated that electrofishing suppression could give cutthroat trout a demographic boost and help them persist longer in sympatry with brook

trout. Both λ and time to extinction increased as the frequency of brook trout suppression increased. In the model, annual suppression ensured that cutthroat trout λ was at least 1.0 and that populations persisted for 50 years, but less-frequent suppression could facilitate persistence ($\lambda \approx 1.0$) under certain conditions (see *Management Recommendations*). Empirical evidence from studies of cutthroat trout (Shepard et al. 2002; Shepard and Nelson 2004) and other salmonids (Moore et al. 1983; Kulp and Moore 2000) demonstrates that greater effort expended to control the nonnative species results in a greater response by the native species.

A counterintuitive model result was that population response depended strongly on the temporal sequence of removal events for a given suppression frequency. Among the tested strategies, use of 2–3 years of consecutive suppression events followed by no more than three consecutive years without suppression was always the most effective. For example, for 20 suppression events over 50 years, scenario 20A (2

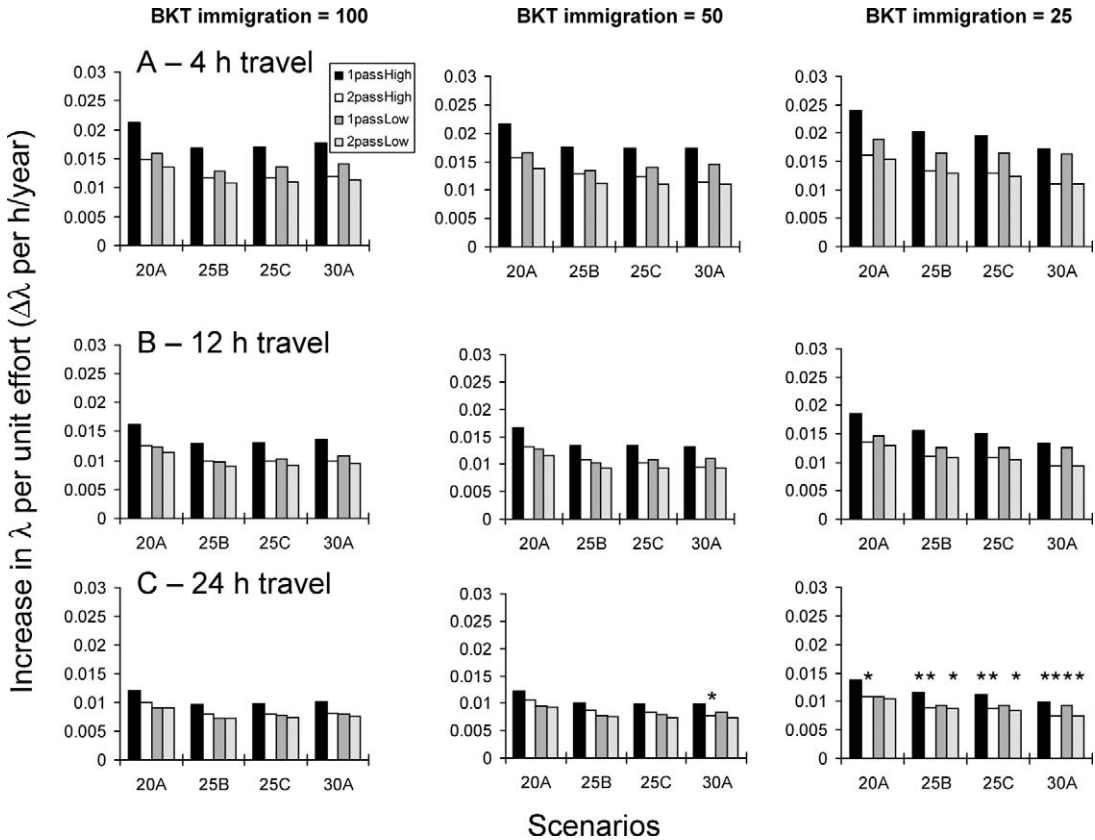


FIGURE 7.—Benefit–cost ratios for increases in median population growth rate (λ) of cutthroat trout per unit of effort (h/year) under four selected nonnative brook trout suppression scenarios (defined in Table 3) applied to a 3-km stream segment under different brook trout immigration rates (25, 50, and 100 fish/year) and crew travel times to and from the site: (A) 4 h, (B) 12 h, and (C) 24 h. Two-pass electrofishing with a low capture probability (2passLow) was not modeled directly, but the effect was estimated as equivalent to one-pass electrofishing with a high capture probability (1passHigh; see Table 2). Asterisks in (C) indicate scenarios for which the distribution of simulated λ predicted a stable cutthroat trout population (i.e., 95th percentile of the distribution was at least 1.0) across all travel times (A–C) for a given level of brook trout immigration. For example, under two-pass suppression and a high capture probability (2passHigh), scenario 30A produced a stable cutthroat trout population when brook trout immigration was 50 fish/year, and the same result also applies to panels A and B for that immigration rate.

years on, 3 years off) was more effective at slowing the decline of cutthroat trout than was scenario 20C (4 years on, 6 years off; Table 4). Marked differences in λ and time to extinction were evident among equal-frequency scenarios as the frequency of suppression increased (e.g., to 30 visits) and the absolute response of cutthroat trout increased (Table 4). Surprisingly, for one scenario (20A), the suppression sequence appeared to compensate for the lower frequency of suppression relative to that of scenario 25A (suppression in alternate years; Table 4).

Biologically, the effect of consecutive years of electrofishing is to temporarily disrupt the recruitment bottleneck caused by brook trout competition or predation so that one or two cohorts of cutthroat trout

can recruit to the adult population, which is relatively unaffected by brook trout (Peterson et al. 2004). Gaps in control efforts that exceeded the generation time of cutthroat trout (~ 5 years/generation in this model) undermined any previous gains. Successful nonnative trout control programs typically result in a pulse of recruitment by native trout, but the pulse may be absent or undetectable unless several successive years of suppression have occurred (e.g., Moore et al. 1983; Thompson and Rahel 1996; Shepard et al. 2002; Peterson et al. 2004). Our model supports the conclusion that consistent, repeated suppression is needed to interrupt the recruitment cycle of nonnative trout by removing adults prior to spawning and removing age-0 fish after they are large enough to be

effectively captured by electrofishing (e.g., Shepard and Nelson 2004). The model is also consistent with reports that wild brook trout populations can quickly recover when suppression is interrupted (Rosenlund et al. 2001), especially when movement from untreated stream reaches is possible (Shepard et al. 2002; Peterson et al. 2004; Meyer et al. 2006).

Brook trout immigration had a significant swamping effect on cutthroat trout response to brook trout suppression in our model. As immigration increased, the suppression frequency and intensity (number of passes) that were required to achieve a given λ or time to extinction also increased. This relationship was not linear under the modeled conditions, and the effect of immigration diminished when the rate was less than 50 fish/year. The absolute magnitude of immigration clearly mediated the effectiveness of suppression, but the timing of such immigration should also be important. For example, adult brook trout that arrive after a fall suppression event could spawn and subsequently interact with cutthroat trout when the fish are concentrated in refuge habitats during winter (e.g., Chisholm et al. 1987; Jakober et al. 1998). On the other hand, brook trout immigrating in early summer may be present later in the season, when age-0 cutthroat trout emerge and are particularly vulnerable to predation (Novinger 2000). Brook trout immigrate at both times (Peterson and Fausch 2003b) and either situation would affect control efforts, but additional data are needed to determine whether immigration during a particular season has disproportionate ecological effects on cutthroat trout.

Management Recommendations

Suppression of brook trout by electrofishing can help native cutthroat trout populations in situations when eradication is not possible or feasible, even if the outcome of control is simply a less-dramatic decline in the native species. What practical advice and strategies can biologists and managers gain from our modeling results to improve their ability to plan and implement successful control programs?

First, the response of cutthroat trout populations is proportional to the suppression frequency but only up to a point, and the interannual timing of suppression is critical. In simulations, persistence of cutthroat trout was ensured by annual suppression, but whether similar benefits could be obtained with less-frequent suppression depended on all the factors influencing suppression effectiveness (i.e., capture probability, number of electrofishing passes, brook trout immigration, and brook trout λ). Although we modeled arbitrary levels of electrofishing frequency, our results strongly support the conclusion that when annual

suppression is not possible, a repeated sequence of at least three consecutive years of removal followed by no more than 2 years without suppression (scenario 30A) is effective at slowing the decline of cutthroat trout in sympatry with brook trout and could even foster longer-term persistence ($\lambda \approx 1.0$) if brook trout immigration is comparatively low (≤ 25 fish/year). Cutthroat trout populations with few individuals may initially require additional attention to increase their abundance, such as multiple electrofishing visits within a year or suppression over five consecutive years, prior to imposing a systematic suppression schedule.

Second, from a benefit–cost perspective, lower-frequency, one-pass suppression was comparatively cost effective unless brook trout were difficult to capture, the brook trout immigration rate was high, or the field sites were remote. For example, one-pass suppression under scenario 20A was generally the most cost-effective alternative when capture probability was 0.60 or greater, regardless of immigration rate. The comparative benefit of lower-frequency, one-pass electrofishing decreased as travel time to the site increased, so this strategy may be most appropriate for streams that can be accessed by vehicles. Although benefit–cost guidelines generally favor suppression of lower frequency and lower intensity, we caution that this analysis compared relative performance of arbitrary scenarios and therefore it should not be the only consideration in planning or executing nonnative species control projects. Higher-frequency, two-pass suppression produced the greatest λ and longest time to extinction for cutthroat trout in the model (i.e., greatest absolute response) and may be appropriate for populations that are in imminent danger of displacement or that are deemed to be of high conservation value. Moreover, if travel time is long relative to electrofishing time, then biologists should consider remaining at the site and conducting a second electrofishing pass, especially if low capture probabilities are observed or suspected.

Third, sufficient resources must be invested in understanding suppression efficiency and brook trout demographic characteristics, especially immigration. The response of cutthroat trout to brook trout suppression was sensitive to both. Even approximate estimates of electrofishing capture probability (through depletion sampling [e.g., White et al. 1982] or mark–recapture [e.g., Rosenberger and Dunham 2005]) and immigration rate (through mark–recapture or trapping; e.g., Gowan and Fausch 1996; Peterson and Fausch 2003b) could promote more-efficient use of resources or indicate the need for alternate tactics. Useful approaches for reducing the strong effect of brook trout immigration might include construction of weirs

(Peterson and Fausch 2003b), use of pheromone attractants to trap fish (Young et al. 2003), or targeting source populations for control (Travis and Park 2004) even if those populations are not directly adjacent to the primary suppression area. To benefit native cutthroat trout, biologists often remove or install migration barriers depending on the relative threats of isolation versus invasion by nonnative trout (Fausch et al. 2006; Rahel 2007; Peterson et al. 2008). Suppression might be facilitated by partial migration barriers that restrict movement during high streamflows (road culverts) or at base flow (perched culverts) or by rock gabions that reduce but do not eliminate upstream movement (Thompson and Rahel 1998). Typically, biologists either remove such structures to restore connectivity or replace them with permanent barriers to isolate cutthroat trout before eradicating nonnative trout.

Finally, consideration should be given to how maintenance control efforts and managing for sympatry fit into an overall conservation strategy. Using piscicides and installing barriers to eradicate nonnative trout are effective methods of protecting cutthroat trout populations that are judged important based on genetic purity or unique traits, but it is unrealistic to think that such efforts will be possible for all populations. Even when possible, successful nonnative trout eradication projects can be undone by reinvasion, either through barrier failure or intentional or deliberate reintroduction (Behnke 1992; Thompson and Rahel 1996; Harig et al. 2000). Suppression could be the lower-cost alternative if there is a significant threat that brook trout will invade an erstwhile successful eradication project. Thus, maintenance control of brook trout may help maintain cutthroat trout populations of high conservation value until eradication becomes technically or socially feasible. Maintenance control also could be used as part of a strategy to preserve a set of populations that are slightly hybridized or of uncertain genetic status (e.g., Allendorf et al. 2004), or so-called conservation populations (e.g., Hirsch et al. 2006). It may have a role in maintaining native cutthroat trout in reaches downstream of barriers; biologists may be interested in later reclaiming these segments and moving the barriers farther downstream. Response to crises may warrant suppression efforts when legal challenges or environmental regulations temporarily preclude use of more-effective management tools (e.g., piscicides) to protect native salmonid populations that are at risk of invasion (Finlayson et al. 2005).

Caveats, Complexities, and Conclusions

The models we constructed provide demographic insight into how brook trout displace inland cutthroat

trout and will help biologists in evaluating maintenance control strategies to promote coexistence. We caution that the inference from these models extends only to small, headwater streams, although such locations represent the majority of occupied habitat for many subspecies of inland cutthroat trout (Young 1995). Also, the analyses included simplifying assumptions and uncertainty about vital rates, ecological relationships (e.g., density dependence, strength of biotic effects from brook trout), and effects of repeated electrofishing. Consequently, results should be interpreted comparatively rather than literally (Beissinger and Westphal 1998). For example, the model may be pessimistic about the resilience of cutthroat trout if the biotic effects of brook trout are lower than presented here or if cutthroat trout fecundity is greater than that presented. Conversely, model results may be optimistic if population-level effects of electrofishing and handling are strong. Monitoring of such suppression or eradication projects could help address these uncertainties. Appropriately scaled field studies that provide additional vital rate estimates for inland cutthroat trout (allopatric or sympatric with nonnative trout) and that quantify whether the strength of biotic interactions with nonnative trout varies by system, ecological context, or cutthroat trout subspecies will also be important for validating and refining models used to assess viability and evaluate management options.

An understanding of life history and population ecology is central to predicting invasion dynamics (Parker 2000; Sakai et al. 2001) and effectively managing impacts (Simberloff 2003; Travis and Park 2004). We found that brook trout λ and immigration rate strongly influenced model-based predictions about the most beneficial and cost-effective suppression strategy. Additional investigation of compensatory responses by brook trout populations that cause them to rebound when suppression is suspended or incomplete (e.g., Rosenlund et al. 2001; Shepard et al. 2002; Meyer et al. 2006) might provide additional insight for improving the design of control efforts.

Our models and the available empirical evidence indicate that the brute force approach of maintenance control of brook trout by electrofishing can benefit cutthroat trout even when the costs of electrofishing are high (Kulp and Moore 2000; Shepard and Nelson 2004), although success may be incremental or may simply produce a stable population at low abundance. It is easier to protect an existing native cutthroat trout population, even if it is sympatric with nonnative brook trout, than to try and reestablish the native population after it has been extirpated (Harig and Fausch 2002). The threat of further brook trout invasion of headwater streams will probably persist, as will budgetary

pressures on fish management agencies, and continuing public misconceptions may occasionally preclude use of preferred eradication methods (i.e., piscicides). Consequently, maintenance control of brook trout and managing for sympatry are likely to remain options for biologists that are working to conserve native cutthroat trout.

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References

- Adams, S. B. 1999. Mechanisms limiting a vertebrate invasion: brook trout in mountain streams of the northwestern USA. Doctoral dissertation. University of Montana, Missoula.
- Adams, S. B., C. A. Frissell, and B. E. Rieman. 2002. Changes in distribution of non-native brook trout in an Idaho drainage over two decades. *Transactions of the American Fisheries Society* 131:561–568.
- Allendorf, F. W., R. F. Leary, N. P. Hitt, K. L. Knudsen, L. L. Lundquist, and P. Spruell. 2004. Intercrosses and the U.S. Endangered Species Act: should hybridized populations be included as westslope cutthroat trout? *Conservation Biology* 18:1203–1213.
- Ball, O. P., and O. B. Cope. 1961. Mortality studies on cutthroat trout in Yellowstone Lake. U.S. Fish and Wildlife Service Research Report 55.
- Behnke, R. J. 1992. Native trout of western North America. American Fisheries Society, Monograph 6, Bethesda, Maryland.
- Beissinger, S. R., and M. I. Westphal. 1998. On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management* 62:821–841.
- Carline, R. F. 2001. Effects of high-frequency pulsed-DC electrofishing on a wild brown trout population. *North American Journal of Fisheries Management* 21:571–579.
- Chisholm, I. A., W. A. Hubert, and T. A. Wesche. 1987. Winter stream conditions and use of habitat by brook trout in high-elevation Wyoming streams. *Transactions of the American Fisheries Society* 116:176–184.
- Clark, M. E., and K. A. Rose. 1997. An individual-based modeling analysis of management strategies for enhancing brook trout populations in southern Appalachian streams. *North American Journal of Fisheries Management* 17:54–76.
- Coleman, M. A., and K. D. Fausch. 2007. Cold summer temperature regimes cause a recruitment bottleneck in age-0 Colorado River cutthroat trout reared in laboratory streams. *Transactions of the American Fisheries Society* 136:639–654.
- Downs, C. C., R. G. White, and B. B. Shepard. 1997. Age at sexual maturity, sex ratio, fecundity, and longevity of isolated headwater populations of westslope cutthroat trout. *North American Journal of Fisheries Management* 17:85–92.
- Dunham, J. B., S. B. Adams, R. E. Schroeter, and D. C. Novinger. 2002. Alien invasions in aquatic ecosystems: toward an understanding of brook trout invasions and potential impacts on inland cutthroat trout in western North America. *Reviews in Fish Biology and Fisheries* 12:373–391.
- Dunham, J. B., D. S. Pilliod, and M. K. Young. 2004. Assessing the consequences of nonnative trout in headwater ecosystems in western North America. *Fisheries* 29(6):18–26.
- Fausch, K. D., B. E. Rieman, M. K. Young, and J. B. Dunham. 2006. Strategies for conserving native salmonid populations at risk from nonnative fish invasions: tradeoffs in using barriers to upstream movement. U.S. Forest Service, Rocky Mountain Research Station, RMRS-GTR-174, Fort Collins, Colorado.
- Finlayson, B. J., R. A. Schnick, R. L. Cailteux, L. Demong, W. D. Horton, W. McClay, and C. W. Thompson. 2002. Assessment of antimycin A use in fisheries and its potential for reregistration. *Fisheries* 27(6):10–18.
- Finlayson, B. J., W. Somer, D. Duffield, D. Propst, C. Mellison, T. Pattengill, H. Sexauer, T. Nesler, S. Gurtin, J. Elliot, F. Partridge, and D. Skaar. 2005. Native inland trout restoration on national forests in the western United States—time for improvement? *Fisheries* 30(5):10–19.
- Gowan, C., and K. D. Fausch. 1996. Mobile brook trout in two high-elevation Colorado streams: re-evaluating the concept of restricted movement. *Canadian Journal of Fisheries and Aquatic Sciences* 53:1370–1381.
- Gresswell, R. E., editor. 1988. Status and management of interior stocks of cutthroat trout. American Fisheries Society, Symposium 4, Bethesda, Maryland.
- Habera, J. W., R. J. Strange, B. D. Carter, and S. E. Moore. 1996. Short-term mortality and injury of rainbow trout caused by three-pass AC electrofishing in a southern Appalachian stream. *North American Journal of Fisheries Management* 16:192–200.
- Harig, A. L., and K. D. Fausch. 2002. Minimum habitat requirements for establishing translocated cutthroat trout populations. *Ecological Applications* 12:535–551.
- Harig, A. L., K. D. Fausch, and M. K. Young. 2000. Factors influencing success of greenback cutthroat trout translocations. *North American Journal of Fisheries Management* 20:994–1004.
- Hilderbrand, R. H. 2003. The roles of carrying capacity, immigration, and population synchrony on persistence of stream-resident cutthroat trout. *Biological Conservation* 110:257–266.
- Hirsch, C. L., S. E. Albeke, and T. P. Nesler. 2006. Range-wide status of Colorado River cutthroat trout (*Oncorhynchus clarkii pleuriticus*): 2005. Colorado Division of Wildlife, Denver.
- Jakober, M. J., T. E. McMahon, R. F. Thurow, and C. G.

- Clancey. Role of stream ice on fall and winter movements and habitat use by bull trout and cutthroat trout in Montana headwater streams. *Transactions of the American Fisheries Society* 127:223–235.
- Kennedy, B. M., D. P. Peterson, and K. D. Fausch. 2003. Different life history of brook trout populations invading mid-elevation and high-elevation cutthroat trout streams in Colorado. *Western North American Naturalist* 63:215–223.
- Kocovsky, P. M., C. Gowan, K. D. Fausch, and S. C. Riley. 1997. Spinal injury rates in three wild trout populations in Colorado after eight years of backpack electrofishing. *North American Journal of Fisheries Management* 17:308–313.
- Kulp, M. A., and S. E. Moore. 2000. Multiple electrofishing removals for eliminating rainbow trout in a small southern Appalachian stream. *North American Journal of Fisheries Management* 20:259–266.
- Larson, G. L., S. E. Moore, and D. C. Lee. 1986. Angling and electrofishing for removing nonnative rainbow trout from a stream in a national park. *North American Journal of Fisheries Management* 6:580–585.
- Lomnický, G. A., T. R. Whittier, R. M. Hughes, and D. V. Peck. 2007. Distribution of nonnative aquatic vertebrates in western U.S. streams and rivers. *North American Journal of Fisheries Management* 27:1082–1093.
- MacCrimmon, H. R., and J. S. Campbell. 1969. World distribution of brook trout, *Salvelinus fontinalis*. *Journal of the Fisheries Research Board of Canada* 26:1699–1725.
- Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* 10:689–710.
- McFadden, J. T., G. R. Alexander, and D. S. Shetter. 1967. Numerical changes and population regulation in brook trout *Salvelinus fontinalis*. *Journal of the Fisheries Research Board of Canada* 24:1425–1459.
- McGrath, C. C., and W. M. Lewis, Jr. 2007. Competition and predation as mechanisms for displacement of greenback cutthroat trout by brook trout. *Transactions of the American Fisheries Society* 136:1381–1392.
- Meyer, K. A., J. A. Lamansky, Jr., and D. J. Schill. 2006. Evaluation of an unsuccessful brook trout electrofishing removal project in a small Rocky Mountain stream. *North American Journal of Fisheries Management* 26:849–860.
- Meyer, K. A., D. J. Schill, F. S. Elle, and J. A. Lamansky, Jr. 2003. Reproductive demographics and factors that influence length at sexual maturity in Yellowstone cutthroat trout in Idaho. *Transactions of the American Fisheries Society* 132:183–195.
- Mills, L. E. 1966. Environmental factors and egg mortality of cutthroat trout, *Salmo clarki*, in three tributaries of Yellowstone Lake. Master's thesis. Colorado State University, Fort Collins.
- Moore, S. E., M. A. Kulp, J. Hammonds, and B. Rosenlund. 2005. Restoration of Sams Creek and an assessment of brook trout restoration methods. U.S. National Park Service Technical Report, NPS/NRWRD/NRTR-2005/342, Fort Collins, Colorado.
- Moore, S. E., B. L. Ridley, and G. L. Larson. 1983. Standing crops of brook trout concurrent with removal of rainbow trout from selected streams in Great Smoky Mountains National Park. *North American Journal of Fisheries Management* 3:72–80.
- Morita, K., and S. Yamamoto. 2002. Effects of habitat fragmentation by damming on the persistence of stream-dwelling charr populations. *Conservation Biology* 16:1318–1323.
- Morita, K., and A. Yokota. 2002. Population viability of stream-resident salmonids after habitat fragmentation: a case study with white-spotted charr (*Salvelinus leucomaenis*) by an individual based model. *Ecological Modelling* 155:85–94.
- Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology. Sinauer, Sunderland, Massachusetts.
- Noon, B. R., and J. R. Sauer. 1992. Population models for passerine birds: structure, parameterization and analysis. Pages 441–464 in D. R. McCullough and R. H. Barrett, editors. *Wildlife 2001: populations*. Elsevier, London.
- Novinger, D. C. 2000. Reversals in competitive ability: do cutthroat trout have a thermal refuge from competition with brook trout? Doctoral dissertation. University of Wyoming, Laramie.
- Novinger, D. C., and F. J. Rahel. 2003. Isolation management with artificial barriers as a conservation strategy for cutthroat trout in headwater streams. *Conservation Biology* 17:1–11.
- Parker, I. M. 2000. Invasion dynamics of *Cytisus scoparius*: a matrix model approach. *Ecological Applications* 10:726–743.
- Paul, A. J., J. R. Post, and J. M. Stelfox. 2003. Can anglers influence the abundance of native and nonnative salmonids in a stream from the Canadian Rocky Mountains? *North American Journal of Fisheries Management* 23:109–119.
- Peterson, D. P., and K. D. Fausch. 2002. Demography, dispersal, and effects of nonnative brook trout on native cutthroat trout in Colorado streams. Final report to Colorado Division of Wildlife, U.S. Department of Interior Central Utah Project Completion Act Office, U.S. Forest Service, and Trout Unlimited. Colorado State University, Fort Collins.
- Peterson, D. P., and K. D. Fausch. 2003a. Testing population-level mechanisms of invasion by a mobile vertebrate: a simple conceptual framework for salmonids in streams. *Biological Invasions* 5:239–259.
- Peterson, D. P., and K. D. Fausch. 2003b. Upstream movement by nonnative brook trout (*Salvelinus fontinalis*) promotes invasion of native cutthroat trout (*Oncorhynchus clarki*) habitat. *Canadian Journal of Fisheries and Aquatic Sciences* 60:1502–1516.
- Peterson, D. P., K. D. Fausch, and G. C. White. 2004. Population ecology of an invasion: effects of nonnative brook trout on native cutthroat trout. *Ecological Applications* 14:754–772.
- Peterson, D. P., B. E. Rieman, J. B. Dunham, K. D. Fausch, and M. K. Young. 2008. Analysis of trade-offs between threats of invasion by nonnative brook trout (*Salvelinus fontinalis*) and intentional isolation for native westslope cutthroat trout (*Oncorhynchus clarkii lewisi*). *Canadian Journal of Fisheries and Aquatic Sciences* 65:557–573.

- Poole, R. W. 1974. Introduction to quantitative ecology. McGraw-Hill, New York.
- Pritchard, V. L., and D. E. Cowley. 2006. Rio Grande cutthroat trout (*Oncorhynchus clarkii virginalis*): a technical conservation assessment. U.S. Forest Service, Rocky Mountain Region, Fort Collins, Colorado. Available: www.fs.fed.us. (September 2006).
- Quinlan, R. E. 1980. A study of the biology of the Colorado River cutthroat trout (*Salmo clarki pleuriticus*) population in the North Fork of the Little Snake River drainage in Wyoming. Master's thesis. University of Wyoming, Laramie.
- Rahel, F. J. 2000. Homogenization of fish faunas across the United States. *Science* 288:854–856.
- Rahel, F. J. 2002. Homogenization of freshwater faunas. *Annual Review of Ecology and Systematics* 33:291–315.
- Rahel, F. J. 2007. Biogeographic barriers, connectivity and homogenization of freshwater faunas: it's a small world after all. *Freshwater Biology* 52:696–710.
- Roghair, C. N., and C. A. Dolloff. 2005. Brook trout movement during and after recolonization of a naturally defaunated stream reach. *North American Journal of Fisheries Management* 25:777–784.
- Rosenberger, A. E., and J. B. Dunham. 2005. Validation of abundance estimates from mark–recapture and removal techniques for rainbow trout captured by electrofishing in small streams. *North American Journal of Fisheries Management* 25:1395–1410.
- Rosenlund, B. D., C. Kennedy, and K. Czarnowski. 2001. Fisheries and aquatic management Rocky Mountain National Park 2001. Rocky Mountain National Park, National Park Service, Estes Park, Colorado.
- Sakai, A. K., F. W. Allendorf, J. S. Holt, D. M. Lodge, J. Molofsky, K. A. With, S. Baughman, R. J. Cabin, J. E. Cohen, N. C. Ellstrand, D. E. McCauley, P. O'Neil, I. M. Parker, J. N. Thompson, and S. G. Weller. 2001. The population biology of invasive species. *Annual Review of Ecology and Systematics* 32:305–332.
- Schade, C. B., and S. A. Bonar. 2005. Distribution and abundance of nonnative fishes in streams of the western United States. *North American Journal of Fisheries Management* 25:1386–1394.
- Shepard, B. B., B. E. May, and W. Urie. 2005. Status and conservation of westslope cutthroat trout within the western United States. *North American Journal of Fisheries Management* 25:1426–1440.
- Shepard, B. B., and L. Nelson. 2004. Conservation of westslope cutthroat trout by removal of brook trout using electrofishing: 2001–2003. Report to Montana Fish, Wildlife and Parks, Helena.
- Shepard, B. B., R. Spoon, and L. Nelson. 2002. A native westslope cutthroat trout population responds positively after brook trout removal and habitat restoration. *Intermountain Journal of Sciences* 8:191–211.
- Simberloff, D. 2003. How much information on population biology is needed to manage introduced species? *Conservation Biology* 17:83–92.
- Simberloff, D., I. M. Parker, and P. N. Windle. 2005. Introduced species policy, management, and future research needs. *Frontiers in Ecology and the Environment* 3:12–20.
- Stapp, P., and G. D. Hayward. 2002. Effects of an introduced piscivore on native trout: insights from a demographic model. *Biological Invasions* 4:299–316.
- Stelfox, J. D., D. M. Baayens, A. J. Paul, and G. E. Shumaker. 2001. Quirk Creek brook trout suppression project. Pages 37–46 in M. K. Brewin, A. J. Paul, and M. Monita, editors. Bull trout II conference proceedings. Trout Unlimited Canada, Calgary, Alberta.
- Thompson, P. D., and F. J. Rahel. 1996. Evaluation of depletion-removal electrofishing of brook trout in small Rocky Mountain streams. *North American Journal of Fisheries Management* 16:332–339.
- Thompson, P. D., and F. J. Rahel. 1998. Evaluation of human-made barriers in small Rocky Mountain streams in preventing upstream movement of brook trout. *North American Journal of Fisheries Management* 18:206–210.
- Travis, J. M. J., and K. J. Park. 2004. Spatial structure and control of invasive alien species. *Animal Conservation* 7:321–330.
- Tripp, D. B., P. T. P. Tsui, and P. J. McCart. 1979. Baseline fisheries investigations in the McLean Creek ATV and Sibbald Flat snowmobile areas, volume I. Report to Alberta Department of Recreation, Parks and Wildlife, Calgary, Alberta, Canada.
- Veléz-Espino, L. A., M. G. Fox, and R. L. McLaughlin. 2006. Characterization of elasticity patterns of North American freshwater fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 63:2050–2066.
- White, G. C., D. R. Anderson, K. P. Burnham, and D. L. Otis. 1982. Capture–recapture and removal methods for sampling closed populations. Los Alamos National Laboratory, Report LA-8787-NERP, Los Alamos, New Mexico.
- Young, M. K. 1995. Conservation assessment for inland cutthroat trout. U.S. Forest Service General Technical Report RM-GTR-256.
- Young, M. K. 2008. Colorado River cutthroat trout: a technical conservation assessment. U.S. Forest Service General Technical Report RMRS-GTR-207-WWW.
- Young, M. K., P. M. Guenther-Gloss, and A. D. Ficke. 2005. Predicting cutthroat trout (*Oncorhynchus clarkii*) abundance in high-elevation streams: revisiting a model of translocation success. *Canadian Journal of Fisheries and Aquatic Sciences* 62:2399–2408.
- Young, M. K., B. K. Micek, and M. Rathbun. 2003. Probable pheromonal attraction of sexually mature brook trout to mature male conspecifics. *North American Journal of Fisheries Management* 23:276–282.